A NEW CROCODILE OF THE GAVIAL ECOMORPH MORPHOLOGY FROM THE MIOCENE OF NORTHERN AUSTRALIA.

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ABSTRACT

Harpacochampsa camfieldensis gen. et sp. nov. from the mid-Miocene Camfield Beds of northern Australia is the first slender-snouted extinct crocodile known from the Australian continent. It is founded on the anterior portion of the snout, posterolateral portion of the cranium and an anterior dentary fragment. *Harpaco- champsa camfieldensis* is distinctive in having highly size-differentiated premaxillary teeth and isodont maxillary teeth. The largest rostral teeth are found on the premaxillae, as in *Gavialis gangeticus*. The relative size and internal morphology of the supratemporal fenestra, and jugal morphology at the level of the infratemporal fenestra, also resemble those of the gavial. The arrangement of the cranial bones differs from that in *Gavialis*, corresponding most closely with extant *Crocodylus* species. Some features present on *Harpacochampsa camfieldensis* have previously been considered diagnostic of gavialids, but are here interpreted to be convergently evolved as part of a functional adaptation. *Harpacochampsa camfieldensis* is shown to be a crocodylid, but its affinities within the group cannot be determined because of incomplete preservation.

KEYWORDS: Crocodilia, Crocodylidae, *Harpacochampsa* gen. nov., *Harpacochampsa camfieldensis* n.sp., new species, fossil form, Miocene, gavial ecomorph, palaeobiology.

INTRODUCTION

Harpacochampsa camfieldensis gen. et sp. nov. from the mid-Miocene Camfield Beds of northern Australia is the first slender-snouted, extinct crocodile known from Australian Cainozoic sediments. It is here compared with *Crocodylus johnstoni* (Krefft), and the extant, long-snouted crocodilians figured by Iordansky (1973): *Crocodylus acutus* Cuvier, *C. cataphractus* Cuvier, *Tomistoma schlegelii* (S. Muller) and *Gavialis gangeticus* (Gmelin).

Harpacochampsa camfieldensis is known primarily from a rostral fragment and the posterolateral portion of the skull. The functional complex retained by these fragments is similar, in general, to that of extant longirostrine crocodilians, but in some details is convergent on the 'truc' gavial, *Gavialis ganget-* *icus*, particularly in the morphology of the supratemporal fenestra, arrangement of the teeth, robustness of the postorbital bar and jugal morphology at the level of the infratemporal fenestra. Although the new fossil does not directly resolve some of the current problems in Eusuchian systematics reviewed below, it may provide some useful clues to the interpretation of morphological character states considered to be of some systematic significance.

Here we follow Norell (1989) in the usage of an informal taxonomy to describe clades of crocodilians characterised by the extant genera as follows: alligatorids (*Alligator, Caiman, Melanosuchus, Paleosuchus*); crocodylids (*Crocodylus, Osteolaemus*); gavialids (*Gavialis*); and tomistomids (*Tomistoma*). For the purposes of discussion we depart slightly
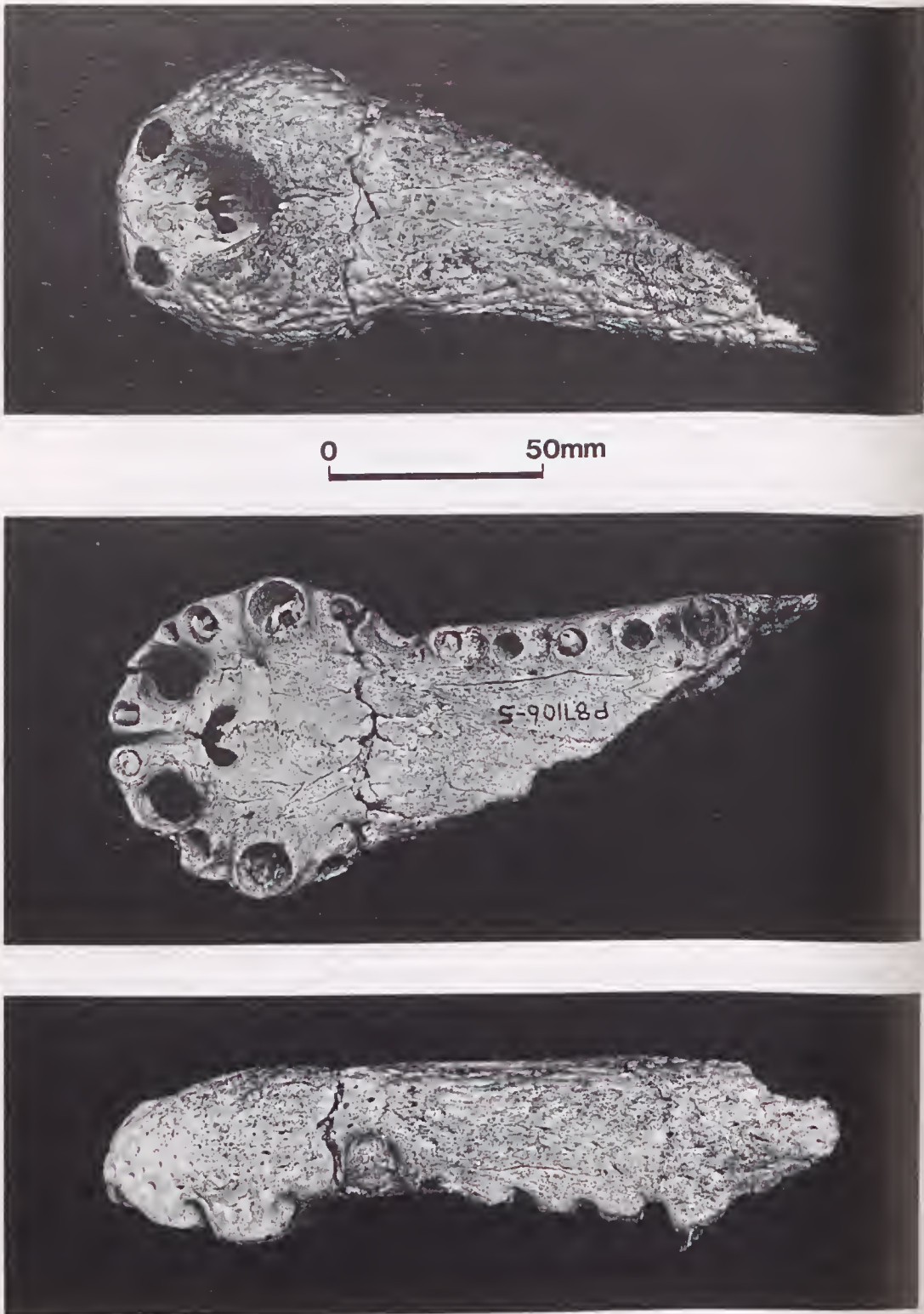
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Fig. 1. *Harpacochampsa camfieldensis* gen. et sp. nov.: anterior snout fragment P87106-5. Abbreviations: **a.p.**, alveolar process or collar; **i.f.**, incisive foramen; **mx**, maxilla; **n**, nasal; **n.f.**, nutrient foramen;
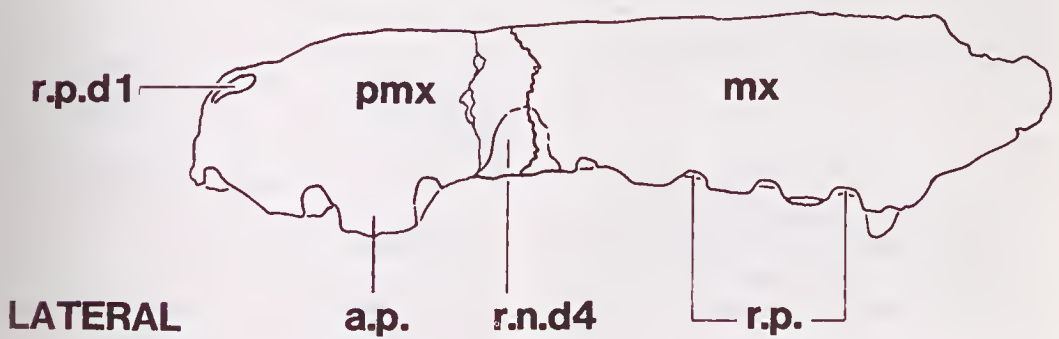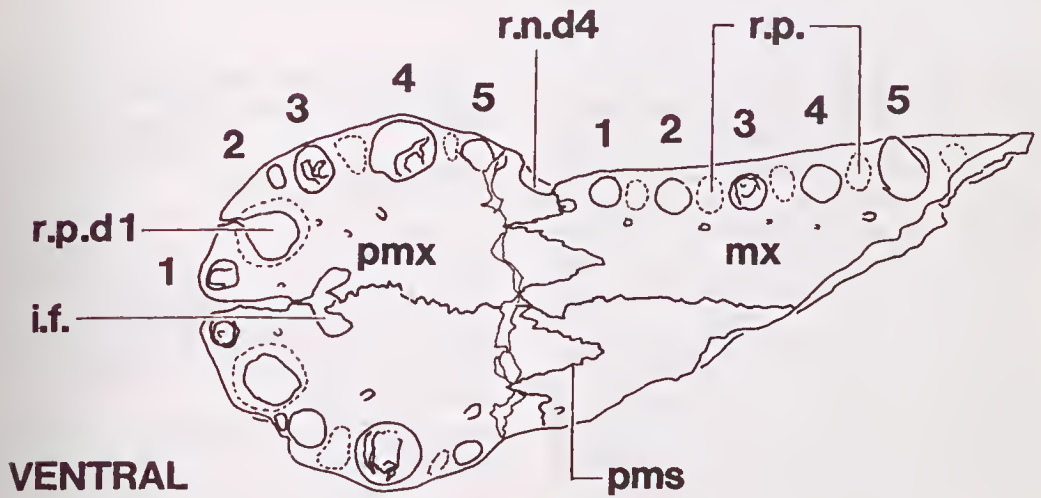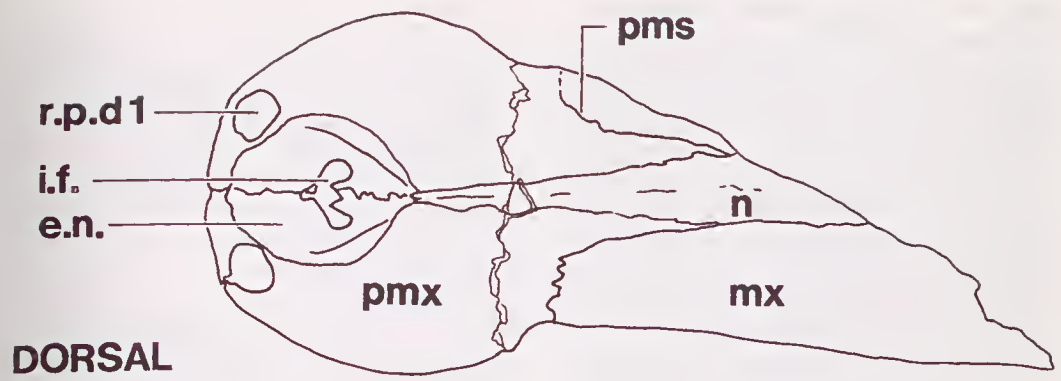
Fig. 1. (cont.): **pms,** premaxillo-maxillary suture; **r.n.d4,** reception notch for fourth dentary tooth; **r.p.d1,** reception pit for first dentary tooth. Premaxillary and maxillary teeth are numbered in sequence from the front.

from Norell (1989) in distinguishing tomisto-mids from crocodylids.

Harpacochampsa camfieldensis is distinct from other fossil crocodilians known from Australia. Its systematic position within the Eusuchia is assessed through an examination of a limited set of morphological character states by which the new fossil, the extant forms listed above, and other extinct Australian genera can be compared.

Four extinct Australian genera are currently recognised: *Pallimnarchus* de Vis from the Pliocene (Molnar 1982a), *Quinkana* Molnar, 1981 from the Pleistocene, *Baru* Willis, Murray and Megirian, 1990 from the late Oligocene to mid-Miocene, and *Australosuchus* Willis and Molnar (in press) from the late Oligocene. Additional mid-Tertiary material, representing at least one additional genus, remains to be described (Willis in prep.). Fragmentary, but presently unassigned, crocodilian material is also known from the Lower Cretaceous and Eocene (Molnar 1982b). Fossilised remains of the living estuarine crocodile, *Crocodylus porosus* are known from the Pliocene (Molnar 1979) and the Australian endemic freshwater crocodile, *C. johnstoni*, is known from the Pleistocene (Willis and Archer 1990). The extinct genera are broad-snouted crocodylids, and although *Quinkana* has a specialised trophic complex (Molnar 1981) convergent on the ziphodonts *Sebecus* and *Pristichampsus*, they most closely resemble the North American taxon *Brachyuranochampsa eversolei* Zangerl, 1944 from the Washakie Eocene (Willis *et al.* 1990). In Willis *et al.* (1990) we advance a tentative hypothesis that the four Australian genera represent an Australian radiation, and together with *Brachyuranochampsa*, possibly form a natural group of crocodylids that are united by the synapomorphic loss of the anterior palatine process. Abbreviations used in the text: NTM, Northern Territory Museum.

SYSTEMATICS

Order CROCODILIA Gmelin
Sub-order EUSUCHIA Huxley
Family CROCODYLIDAE Cuvier
Sub-family CROCODYLINAE Kälin
Genus *Harpacochampsa gen. nov.*

Type species. *Harpacochampsa camfieldensis* sp. nov.

Diagnosis. Crocodylid with robust cranium, but probably long and slender; cranial table proportionally wider and supratemporal fenestrae proportionally larger than in extant *Crocodylus* sp.; premaxillary outline round rather than elliptical as in extant longirostrine *Crocodylus* sp., external nares longer than wide and placed well forward in the premaxillae; five premaxillary teeth varying greatly in size (pseudoheterodont), fourth premaxillary tooth largest in upper series and substantially larger than fifth maxillary tooth; five anterior maxillary teeth of similar size; first dentary tooth as large as the fourth premaxillary tooth.

Etymology. *Harpaco* (Greek), seize; *champsos* (Greek), crocodile, here feminised for euphony; hence *Harpacochampsa*. The generic name alludes to the enlarged premaxillary teeth and their presumed function.

Harpacochampsa camfieldensis sp.nov.
(Figs 1-9)

Type material. HOLOTYPE - NTM P87106-1, posterolateral portion of the skull with part of the neurocranium; NTM P87106-5, anterior portion of the rostrum including both premaxillae and the left maxilla to a point just behind the fifth maxillary tooth; NTM P87106-6, tip of the right dentary with alveoli for the first and second dentary teeth; NTM P87106-19 and NTM P87106-20, osteoderms.

Type locality and stratigraphy. *Harpacochampsa camfieldensis* is a new addition to the Bullock Creek Local Fauna and was collected from the Camfield Beds at a locality about 25km southeast of Camfield Homestead in the north central Northern Territory (Plane and Gatehouse 1968). The Camfield Beds consist of fluvial and lacustrine calcareous conglomerates, calcarenites and calcilutites. Based primarily on the stage of evolution of diprotodontid marsupials of the Bullock Creek Local Fauna, the Camfield Beds are interpreted to be younger than the Wipijiri Formation (Kutjumarpu Local Fauna) of South Australia, and older than the Waite Formation (Alcoota Local Fauna) of the southern Northern Territory. Woodburne *et al.* (1985) estimate a mid-Miocene age for the Camfield Beds. The fossils were extracted from their matrix using acetic acid.

Description and expression of morphological character states. The anterior portion

Crocodylus acutus

C. johnstoni

C. cataphractus

Tomistoma schlegelii

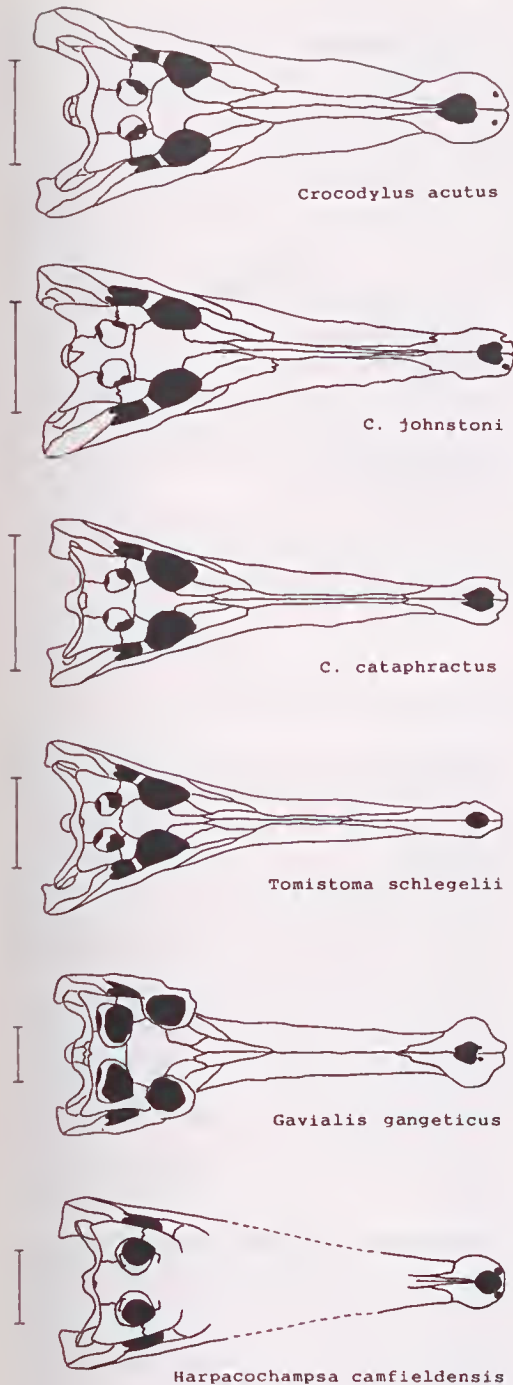Gavialis gangeticus

Harpacochampsa camfieldensis

Fig. 2. Partial restoration of *H. camfieldensis* in dorsal view compared with extant crocodilians: *C. acutus*, *C. cataphractus*, *T. schlegelii*, and *G. gangeticus* after lordansky (1973: figs 1, 2, 3 and 5 respectively); *C. johnstoni* from NTM CM15. Scale bars are each 100mm long.

of the snout of *H. camfieldensis* P87106-5 (Fig. 1) is generally similar to that in the slender-snouted living members of the genus *Crocodylus*: the sutural relationships and general degree of robustness most closely match *C. acutus* (Fig. 2), though the maxillary portion of the snout is narrower (Fig. 3, Table 1). The rostrum is stoutly constructed and proportionally deep for its width. At the level of the fifth maxillary tooth the transverse cross-section is a recumbent D-shape, with a flat palate, vertical sides, strongly convex dorsolateral curvature and a flattened dorsal segment.

In dorsal and ventral views the premaxillae have a circular outline, modified by the sutural contacts with other bones of the skull. On the palate, the combined premaxillo-maxillary sutures are W-shaped. The sutures pass dorsally up the lateral surfaces of the rostrum, bisecting the well-developed lateral notches for the presumed caniniform fourth dentary teeth. On the dorsal surface, just short of the nasal bones, the suture swings posteromedially for about 25mm before contacting the nasals. This arrangement results in a short, spinose, posterior premaxillary projection lying against the nasals and separating them from the anterior part of the maxillae.

The narial aperture is small, centred well forward on the dorsal premaxillary surface and is slightly longer (33mm) than it is wide (28mm). The nasals enter the aperture at its extreme posterior margin. The incisive foramen is small and roughly crescentic. In dorsal view, the left maxilla widens to a maximum at the fifth maxillary tooth, over which there is a low, but distinct, swelling.

The most distinctive feature of *H. camfieldensis* is its rostral dental array, at least as it may be deduced from the arrangement and dimensions of the alveoli and few remaining teeth. The damaged fifth maxillary tooth, erupted shortly before death, is the only functional tooth present. It is broken within its alveolus, now pointing ventrolaterally rather than ventrally. The base of the tooth is round, while the crown is vertically fluted and has distinct anterior and posterior carinae. The tip is broken off, but the crown was probably long and slender. The broken replacement teeth preserved in some alveoli are similar, but provide no additional useful information on crown morphology. All the alveoli are circular, including the three preserved on the posterior
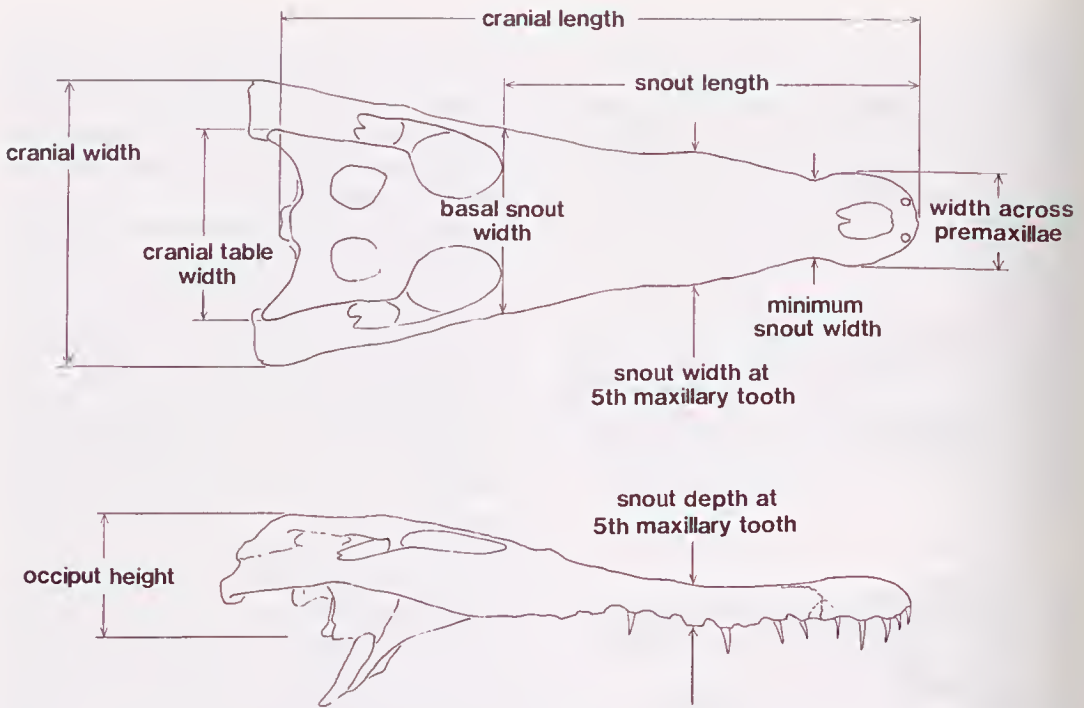
Fig. 3. A crocodile skull showing the positions at which measurements were taken to calculate proportions listed in Table 1.

portion of maxilla with P87106-1. In croco-diles, the posterior maxillary alveoli are often laterally compressed.

Based on alveolar dimensions, the premax-illary teeth of *H. camfieldensis* were highly size-differentiated (pseudoheterodont) while the maxillary teeth were relatively uniform in size, with the fifth maxillary tooth showing about the same degree of enlargement com-pared to the first maxillary tooth as in *C. johnstoni*. The fourth premaxillary alveolus of *H. camfieldensis* has a diameter half as great again as that of the fifth maxillary tooth, in contrast to the typical crocodylid condition in which the fifth maxillary tooth is the largest of the upper series, or alligatorids in which the fourth maxillary tooth is the largest. Only in *G. gangeticus* are some premaxillary teeth larger than the maxillary ones, but there is signifi-cantly less size variation in the premaxillary ones. On the premaxilla of *H. camfieldensis* the second tooth was the smallest, while the first and fifth were both about the size of the first. The third premaxillary tooth was similar in size to the fifth maxillary tooth. Its alveolus, like that of the fourth, is expanded into a prominent collar or alveolar process. All max-illary alveoli have weakly developed collars.

When the jaws were closed, the lower teeth occupied reception pits between the uppers in an 'interbite' arrangement. The first dentary teeth (Fig. 4) were as large as the fourth premaxillary teeth and were received in pits lying between the first and second premaxillary teeth. They breached the dorsal premaxillary surface, anterolaterally to the narial aperture. The fourth mandibular teeth slotted into lateral notches at the maxillo-premaxillary suture in the usual crocodylid arrangement. Judging from the morphology of the the reception pits, none of the other dentary teeth passed up the sides of the rostrum as in some longirostrine piscivorous forms (eg *C. johnstoni*) with needle-like teeth (Fig. 5).

Photographs and line drawings showing struc-ture of the posterolateral cranial fragment P87106-1 are presented in Figure 6. The cra-nial table is flat. When complete, it was pro-portionally broader, with larger supratemporal fenestrae, than in *Crocodylus* species and *T. schlegelii*, but did not exceed *G. gangeticus* (Fig. 2, Table 1). Amongst fossil gavials, the relative size of the supratemporal fenestra most closely resembles *Gavialis lewisi* Lull (1944: fig. 1). The supratemporal fenestra is smoothly confluent with the temporal fossa,

and without horizontal projection of the parietal or squamosal into the fenestra below the level of the skull table. The opening of the orbito-temporal artery in the posterior wall of the supratemporal fenestra is slit-like. These features correspond with *G. gangeticus* and contrast with other crocodilians. The frontal does not contribute to the fenestra margins. In dorsal view the cranial table is convex laterally, unlike extant *Crocodylus* species, where it is straight or concave. Because of the broad skull table, the otic meatus is deeply recessed.

Other similarities with *G. gangeticus* can be seen in lateral view (Figs 6d, 7). The jugal is straight and gracile at the level of the long and narrow infratemporal fenestra and the articular surface of the cranio-mandibular joint faces posteriorly rather than declining posteroventrally. The postorbital bar is proportionally robust, but lacks the post-orbital spine characteristic of *G. gangeticus*. Although damaged and slightly displaced, the pterygoid flange was short, and when complete, projected ventrally at a steep angle (Fig. 6d).

In the new fossil, the cranio-mandibular articulation of the quadrate has prominent dorsal and ventral flanges best seen in lateral view, but there are also clear signs of pathological damage to the articular surface medially (Fig. 6c). The medial half of the articular surface is irregular, rather than smoothly rounded, and a trabecular exostosis extends onto the dorsal margin. The extent to which disease has modified the shape of the articular surface of

Table 1. Skull proportions of *Harpacochampsa camfieldensis* compared with long-snouted living crocodilians. The position of measurements are shown in Figure 3. Bracketed measurements for *H. camfieldensis* are based on the restoration shown in Figure 2: *C. acutus, C. cataphractus, T. schlegelii* and *G. gangeticus* calculated from Iordansky (1973, Figs. 1, 2, 3 and 5 respectively); *C. johnstoni* from NTM CM15.

| SKULL PROPORTION	SPECIES					
	C. acutus	*C. johnstoni*	*C. cataphractus*	*T. schlegelii*	*G. gangeticus*	*H. camfieldensis*
cranial width cranial length x 100	48	43	39	41	38	[41]
basal width of snout snout length x 100	43	36	33	37	28	[41]
snout length cranial length x 100	68	72	71	72	73	[68]
width cranial table cranial width x 100	60	54	63	61	77	66
width supratemporal fenestra width cranial table x 100	25	27	22	25	34	29
height of occiput cranial width x 100	46	48	-	44	49	41
minimum snout width width across premaxillae x 100	85	65	57	69	61	68
snout depth at 5th maxillary tooth snout width at 5th maxillary tooth x 100	37	52	-	56	42	59
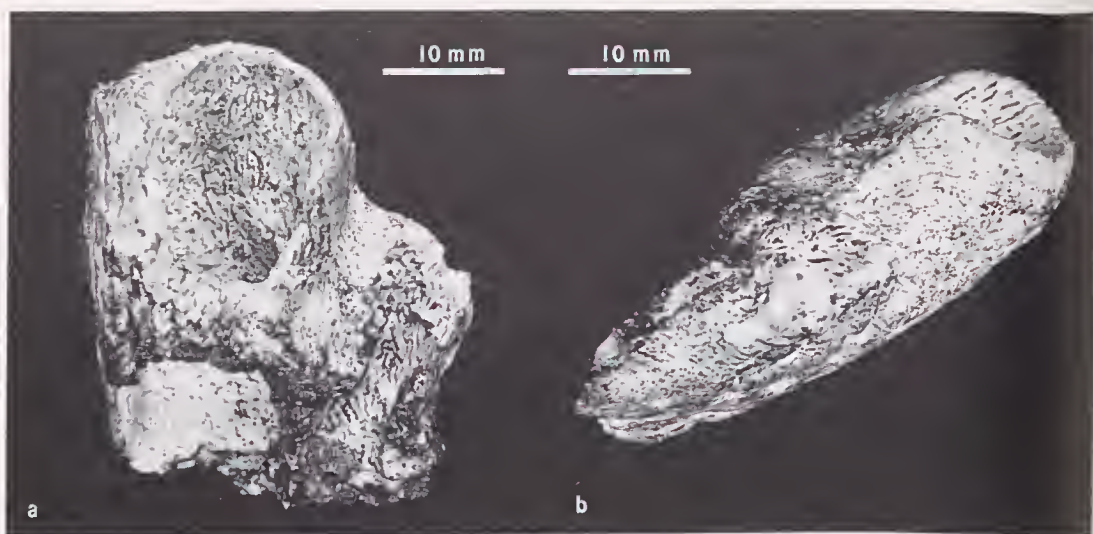
Fig. 4. *Harpacochampsa camfieldensis* gen. et sp. nov.: anterior tip of the right dentary, P87106-5, in (a) occlusal view, anterior towards the top of the page, and (b) left lateral view.

the quadrate on NTM P87106-1 cannot be determined without comparative *Harpaco-champsa* specimens, but the degree of development of the dorsal and ventral flanges may be related in part to the diseased condition and may not reflect a significant functional variation. Similar exostoses are present in some NTM *C. porosus* skulls.

Sutural relationships of the lateral neurocranium (Fig. 6e) fall within the range of *Crocodylus* species (Iordansky 1973, and NTM specimens), but like extant *Crocodylus* species, differ from *Tomistoma* in the reduced exposure of the prootic around the foramen ovale. Basisphenoid exposure in the Camfield crocodile is also relatively large, but not outside the range of *C. porosus* specimens. *Gavialis* also has large prootic exposure, but more strikingly presents a wide exoccipital exposure in lateral view (Iordansky 1973; Tarsitano *et al.* 1989). Similar structure is also recognised in hatchlings of some other crocodilian taxa, but in their ontogeny, the proportional lateral exposure of the pro-otic, basisphenoid and exoccipital is reduced through allometric changes. Tarsitano *et al.* (1989) refer to this process as cranial 'verticalisation'. While the Camfield crocodile shares features with *G. gangeticus* as described above, its neurocranium is fully 'verticalised', including the position and orientation of the internal nares (Fig. 6b). The narial passage at the level of the neurocranium

is a simple tube, as in *C. johnstoni* and *C. porosus*, and *H. camfieldensis* lacks the associated air sinuses that ramify the pterygoid flange in *Gavialis*, or pass up the sides of the neurocranium in *Alligator*. Sutural relationships and proportions seen in other views of P87106-1 also correspond closely with extant *Crocodylus* species.

With few exceptions, the development of other structures fall within the range for extant *Crocodylus* species. On the occipital surface, the fossae for the insertions of M. depressor mandibulae and M. obliquus capitis magnus are separated by a relatively well-developed crest, while the paroccipital process is quite broad in dorsal view. Homologous structures are readily identified on *Crocodylus*, *Gavialis* and *Alligator*. Their degree of development is most probably related to age or function.

In *H. camfieldensis* there is a well-developed vacuity within the parietal above the anterior neurocranium, in a slightly parasagittal position (Fig. 6f). In the portion preserved, there is no indication that this vacuity was connected to the ramifications of the Eustachian system within the bones of the skull. Its relative size and position corresponds to a similar, tissue-filled structure observed by Tarsitano *et al.* (1989) in *Gavialis gangeticus*. In the gavial it also does not appear to be part of the Eustachian system. The function of this organ and its systematic significance are not known.
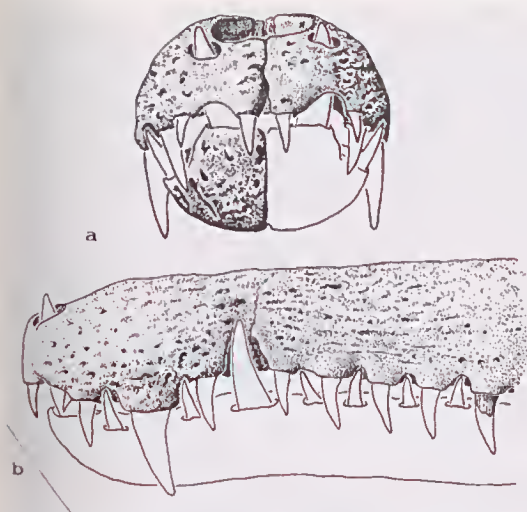
Fig. 5. Partial restoration of the anterior segment of the snout based on P87106-5 and P87106-6: (a) anterior view, (b) lateral view.

Two osteoderms (P87106-19 and P87106-20) are similar to the dorsal osteoderms of *C. johnstoni* (Fig. 8). Both were in sutural contact with adjacent osteoderms of their respective transverse rows. P87106-19 has a suture on one side only, thus occupying a marginal position while P87106-20 occupied an intermediate position in its row. In both osteoderms the anterior and posterior margins taper to a sharp edge, as does the lateral edge of the marginal osteoderm. The dorsal sculpture consists of fairly regularly-sized, circular pits while the internal surface is smooth. The marginal osteoderm has a dorsal longitudinal crest, but the intermediate one is flat. As in *C. johnstoni*, the dorsal osteoderms of *H. camfieldensis* probably formed a complete shield, with successive transverse rows in close approximation.

Etymology. The new species is named "camfield-ensis" (Greek), refering to the Camfield Beds from which it was recorded.

DISCUSSION

Comparison of character states.. Eusuchian systematics are poorly resolved and currently under active debate (Densmore 1983, Densmore and Owen 1989, Buffetaut 1985, Tarsitano *et al* 1989, Norell 1989). We limit ourselves here to a consideration of the few morphological character states by which the new taxon can be compared with extant crocodilians, Australian

fossil genera, and *Brachyuranochampsa*. The suite of character states selected (Table 2) is hardly satisfactory for resolving relationships within the Eusuchia at the level of crocodylids, alligatorids, and gavialids but provides a foundation for the discussion which follows, and permits a conclusion about the higher level affinities of *Harpacochampsa camfieldensis*. The monophyly of Eusuchia is accepted (Benton and Clark 1988) and character-state polarities are selected from the literature. Recent discussions on the systematic significance of Eusuchian character states may be found in Molnar (1981), Buffetaut (1985) and Norell (1989). Iordansky (1973), Steel (1973) and Kälin (1955) are also useful sources.

1. *Posterior intrapterygoid position of the internal nares.* Considered a synapomorphy of the Eusuchia (Benton and Clark 1988), distinguishing them from more archaic crocodilians traditionally referred to as the Protosuchia and Mesosuchia.

2. *The postorbital spine.* Its presence is typically associated with gavialids, but is also present in juvenile *Tomistoma*. Buffetaut (1985) regards its presence as a derived condition, while Norell (1989) presents evidence that the spine is present in embryos and post-hatchlings of other Eusuchians and is lost in ontogeny. We adopt Norell's (1989) interpretation that loss is the derived condition.

3. *Prootic exposure around foramen ovale.* The interpretation of the polarity of this character state is problematic. The condition is evidently primitive in Crocodylia (Iordansky 1973; Norell 1989) but its expression appears to be related to allometric changes that occur during post-embryonic development (Iordansky 1973; Tarsitano *et al.* 1989). Buffetaut (1985) regards large exposure as a derived condition. Norell (1989) provides a useful review and discussion, suggests that insufficient information is currently available to interpret polarity, but prefers to consider the loss of prootic exposure as the derived condition. We use Norell's (1989) polarity in Table 2, and discuss the implications further below.

4. *Lateral exposure of the basisphenoid.* The amount of lateral exposure of the basisphenoid (and the exoccipital) on the braincase wall is probably also related to ontogenetic allometric changes (Iordansky 1973; Tarsitano *et al.* 1989; Norell 1989). It seems probable that the expression of this character is not independent of

Fig. 6. a-c, *Harpacochampsa camfieldensis* gen. et sp. nov.; posterolateral portion of the skull, P87106-1 in:
(a) dorsal view, (b) ventral view, INSET: interpretation of muscle scars on the ventral surface of the quadrate, A, B and B' follow the terminology of Iordansky (1973), (c) posterior view. Abbreviations: **alv**, alveoli for posterior maxillary teeth; **blty**, tympanic bulla; **bo**, basioccipital; **bs**, basisphenoid; **ch**, choana; **cmj**, articular surface of the crano-mandibular joint; **co**, occipital condyle; **ec**, ectopterygoid; **eo**, exoccipital; **fae**, foramen aerium; **fca**, foramen for anterior carotid artery; **fcp**, foramen for the posterior carotid artery; **fEu**, Eustachian foramen; **fit**, infratemporal fenestra; **fm**, foramen magnum; **fMdm**, fossa for the insertion of M. depressor mandibulae;
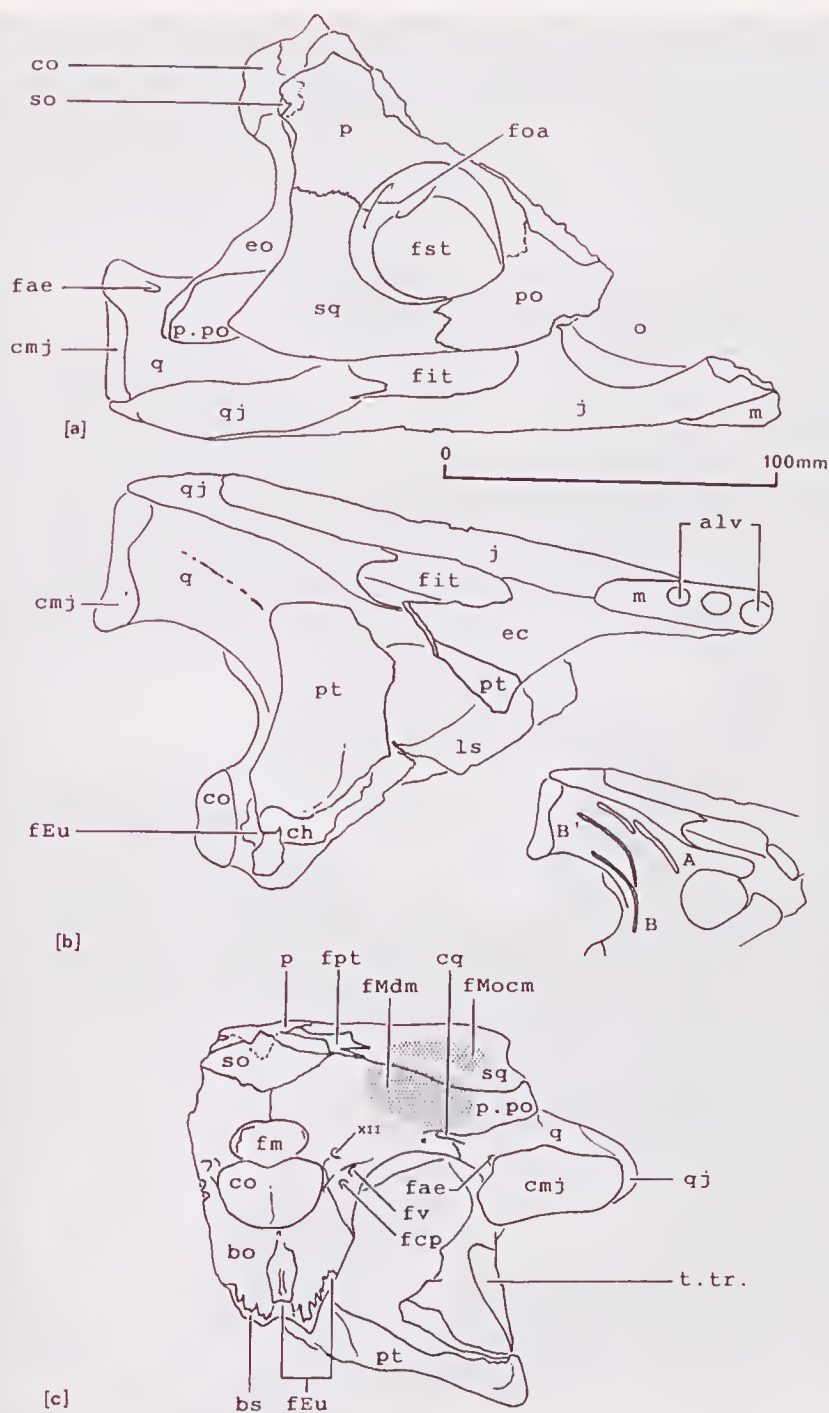
Fig. 6. a-c, (cont.): **fMocm**, fossa for the insertion of M. obliquus capitus magnus; **foa**; foramen for temporo-orbital artery; **fpt**, postemporal fenestra; **fv**, foramen vagi; **fst**, supratemporal fenestra; **in. ot.**, incisura otica; **j**, jugal; **ls**, laterosphenoid; **m**, maxilla; **n.p.**, ?neural pocket of Tarsitano *et al.* (1989); **p**, parietal; **po**, postorbital; **pot** , pro-otic; **p.p.**, ?posterior pocket of Tarsitano *et al.* (1989); **p.po**, paroccipital process; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **so**, supraoccipital; **sp.qj**, quadratojugal spine; **t.tr.**, torus transiliens of the pterygoid; **iv - xii**, foramina for cranial nerves. Hatchures distinguish the Eustachian system.

Fig. 6. d-f, *Harpacochampsa camfieldensis* gen. et sp. nov : posterolateral portion of the skull, P87106-1 in: (d) left lateral view, (e) left ventro-lateral view to show structure of the neurocranial wall, and (f) medial view showing internal structure. Abbreviations: **alv**, alveoli for posterior maxillary teeth; **blty**, tympanic bulla; **bo**, basioccipital; **bs**, basisphenoid; **ch**, choana; **cmj**, articular surface of the crano-mandibular joint; **co**, occipital condyle; **ec**, ectopterygoid; **eo**, exoccipital; **fae**, foramen aerium; **fca**, foramen for anterior carotid artery; **fcp**, foramen for the posterior carotid artery; **fEu**, Eustachian foramen; **fit**, infratemporal fenestra; **fm**, foramen magnum; **fMdm**, fossa for the insertion of M. depressor mandibulae;
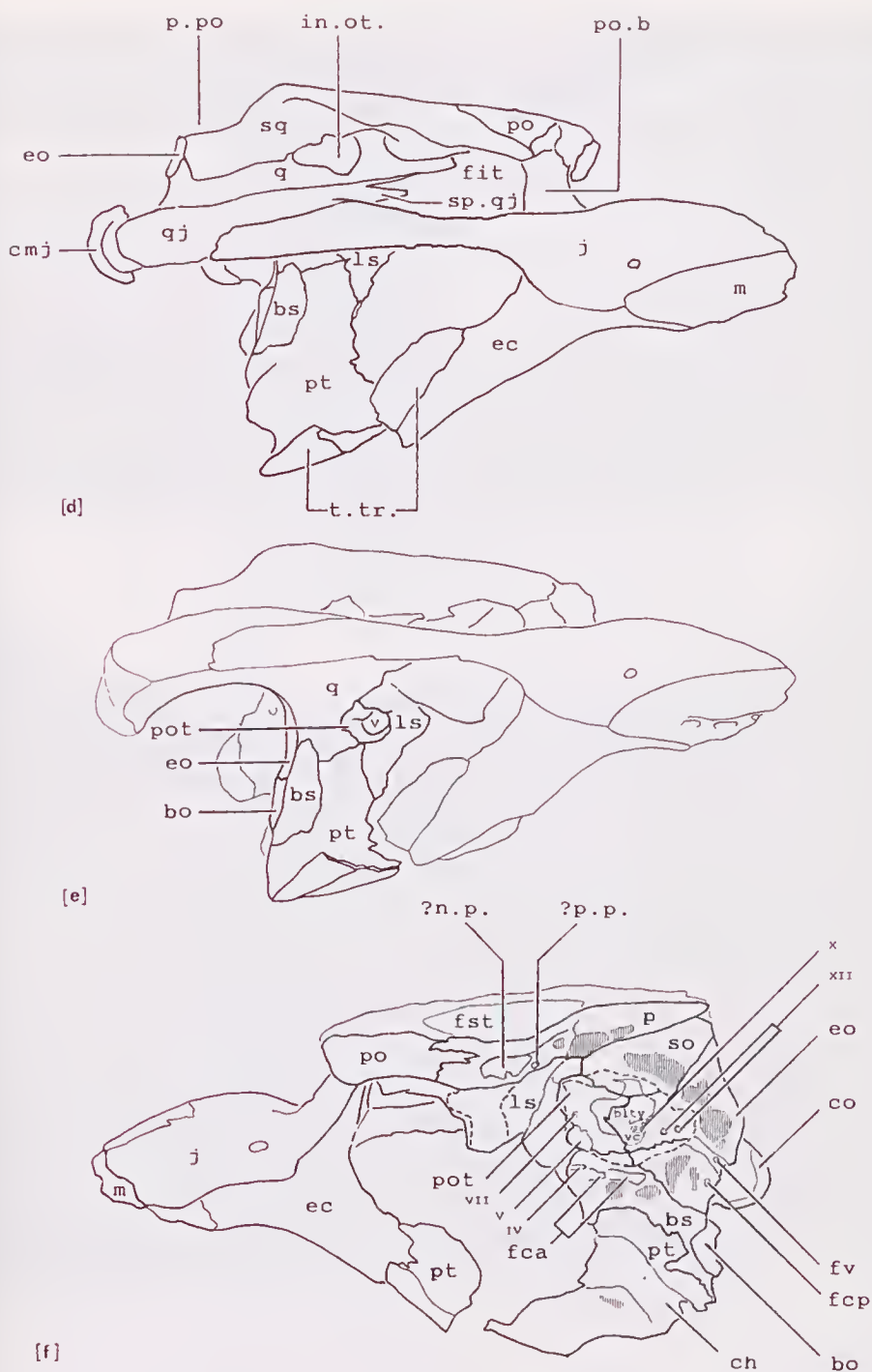
Fig. 6. d-f, (cont.): fMocm, fossa for the insertion of M. obliquus capitus magnus; foa; foramen for temporo-orbital artery; fpt, postemporal fenestra; fv, foramen vagi; fst, supratemporal fenestra; in. ot., incisura otica; j, jugal; ls, laterosphenoid; m, maxilla; n.p., ?neural pocket of Tarsitano *et al.* (1989); p, parietal; po, postorbital; pot, pro-otic; p.p., ?posterior pocket of Tarsitano *et al.* (1989); p.po, paroccipital process; pt, pterygoid; q, quadrate; qj, quadratojugal; so, supraoccipital; sp.qj, quadratojugal spine; t.tr., torus transiliens of the pterygoid; iv - xii, foramina for cranial nerves. Hatchures distinguish the Eustachian system.
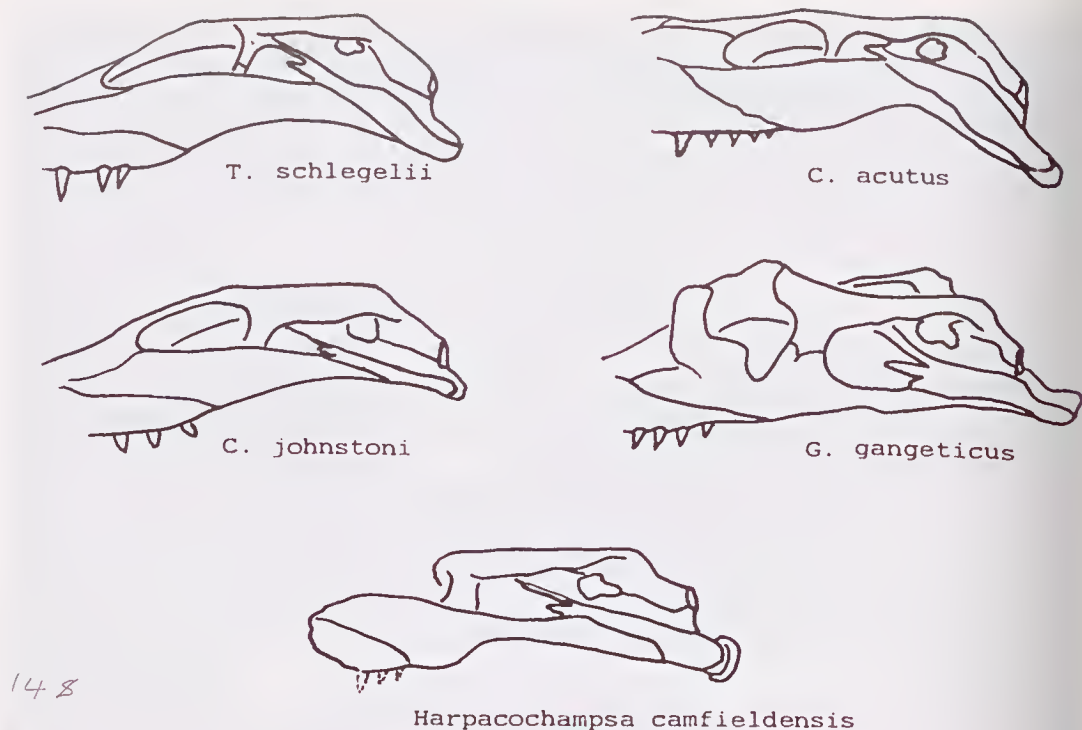
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Fig. 7. Comparisons of the lateral cranial arcade of crocodilian taxa. *C. acutus, T. schlegelii*, and *G. gangeticus* after Iordansky (1973: figs 1, 3 and 5); *C. johnstoni* after NTM CM15; *H. camfieldensis* image (P87106-1) is reversed.

character state 4. Norell (1989) and Buffetaut (1985) take contrary views on polarity, but are respectively consistent with their interpretation of character state 4. For consistency we here follow Norell (1989) and regard reduced basisphenoid exposure as the derived condition.

5. *Posterior process of the ectopterygoid.* Norell (1989) observes that in alligatorids and gavialids the ectopterygoid projects posteriorly in the form of a process along the medial surface of the jugal. He considers its loss to be the derived condition. It has evidently been lost independently in *Alligator*, but other alligatorids retain the primitive state (Norell 1989).

6. *Posterodorsal angle of the infratemporal fenestra.* In crocodylids and tomistomids the quadratojugal-jugal suture contacts the infratemporal fenestra at, or very close to, the posterior angle of the fenestra. In alligatorids and gavialids the quadratojugal-suture lies relatively further forward so that the posterior angle of the infratemporal fenestra is composed entirely of quadratojugal. Norell (1989) regards the condition in crocodylids to be derived.

7. *Reception pit for the fourth dentary tooth.* Alligatorids typically accomodate the caniniform fourth dentary tooth in a reception pit in the rostrum so that when the jaws are closed this tooth is not visible in lateral view. In contrast, the rostrum of other Eusuchians is notched at the maxillo-premaxillary suture so that the fourth dentary tooth remains visible when the jaws are closed. Although there is some variation in this feature in fossil alligatorids and crocodylids, it has a high level of consistency in extant forms. We follow Steel (1973) in his interpretation of a reception pit as the derived condition.

8. *Enlarged fourth maxillary tooth.* In alligatorids the fourth maxillary tooth is the largest in the maxilla. In contrast, in other Eusuchians the fifth maxillary tooth is the largest. Again, there is some inconsistency in the expression of this character in some fossil forms but it serves to distinguish alligatorids, and we interpret the enlarged fourth tooth as the derived condition.

9. *The quadratojugal spine.* Its absence is widely accepted as a characteristic of alligatorids. Buffetaut (1985) interprets its presence as
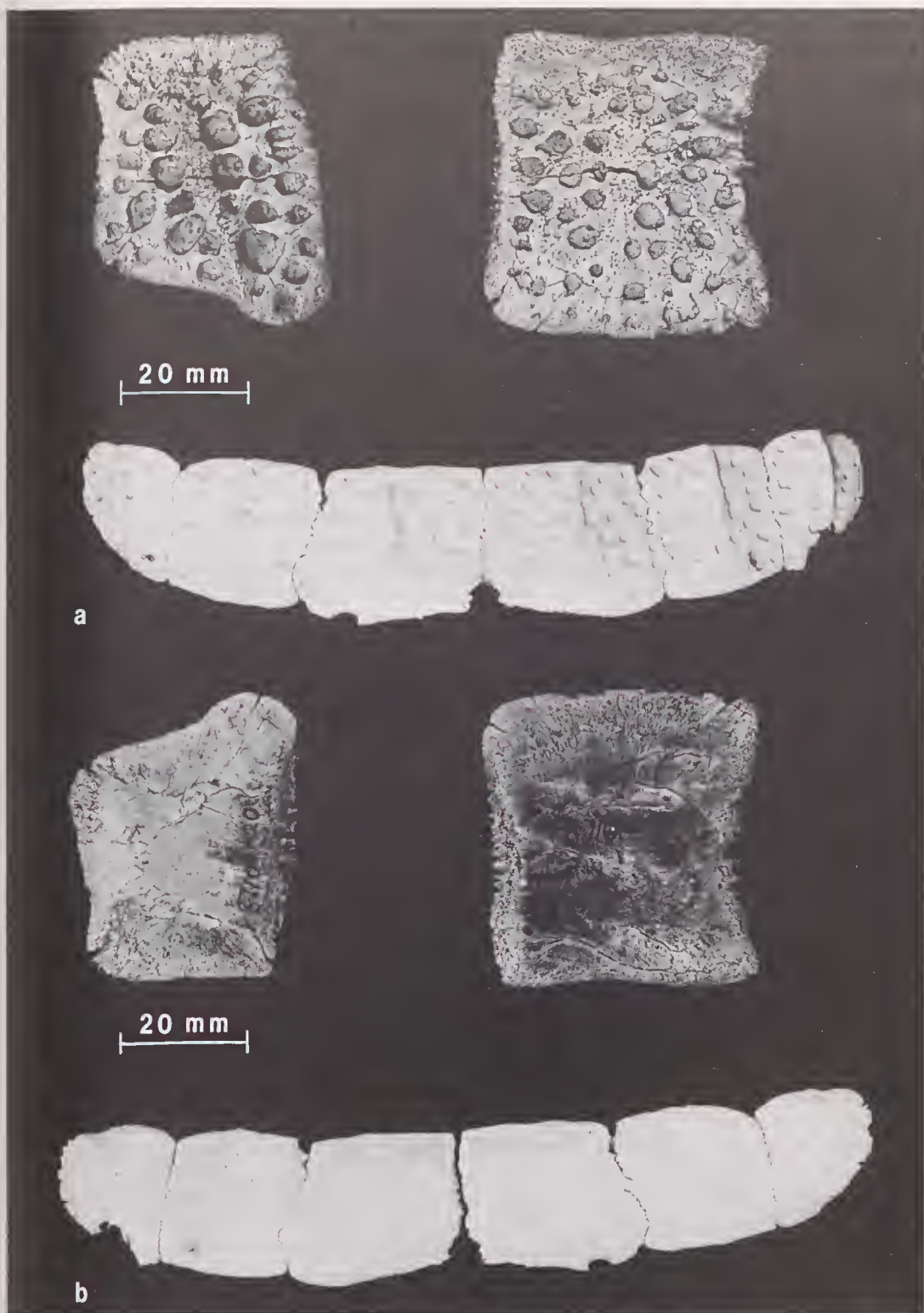
Fig. 8. *Harpacochampsa camfieldensis*, dorsal osteoderms compared with a complete transverse row from *C. johnstoni*; (a) dorsal view, (b) ventral (internal) view.

the derived condition. while Norell (1989) argues that its loss or reduction is derived. Here we accept Norell's (1989) interpretation of polarity. Interestingly, Zangerl (1944:81) observes that while the quadratojugal of *Brachyuranochampsa* more closely resembles 'crocodyloids' than 'alligatoroids', it is doubtful that a quadratojugal spine is present in *Brachyuranochampsa*. Its apparent loss in *Brachyuranochampsa* is considered to be independently derived.

10. *Reduced anterior palatine process.* Typically in Eusuchians, the palato-maxillary suture projects anteriorly as a lobe on the palate which extends beyond the anterior margin of the palatal fenestrae. In some taxa this process is pointed, rather than lobate. In *Brachyuranochampsa* and Australian fossil genera the process is lacking; the palato-maxillary suture is more or less transverse and lies posterior to the anterior margin of the palatal fenestrae (Zangerl 1944; Willis *et al.* 1990). We interpret the loss of the process as a derived feature. Zangerl (1944) considered the palato-maxillary suture of *Brachyuranochampsa* to most closely resemble that of *Tomistoma*.

11. *Interlocking dentition.* Of the living Eusuchia, only *Gavialis, Tomistoma, Osteolaemus* and *Crocodylus* have interlocking upper and lower teeth (interbite). Longirostrine crocodilians usually have an interbite, and this condition has probably evolved independently many times as part of a trophic adaptation for piscivory. Amongst broad-snouted crocodilians, only *Crocodylus* and *Osteolaemus* have an interbite: alligatorids and most broad-snouted fossil crocodylids have the upper teeth closing lateral to the dentary teeth in an 'overbite' arrangement. Lull (1944), for example, traces this evolution in Asian gavialids from the short-snouted *G. breviceps* Pilgrim from the Miocene Bugti Hills of Baluchistan, which he interpreted as being structurally primitive. This character is of limited systematic use because trophic specialisation in longirostrine forms overprints it in many cases, but it is introduced in support of the distinction of the Australian broad-snouted genera and a *Osteolaemus* + *Crocodylus* group. An interbite is considered the derived condition, an interpretation also favoured by Molnar (1981).

The derived conditions for five of the eleven character states listed above are interpreted here to have resulted from the loss of the particular feature. In cladistic methodology, the loss of a feature is generally considered to be of lesser systematic value because losses in different taxa may have occurred independently: once the feature has gone, a common heritage cannot be readily demonstrated. The general conservatism of the Eusuchian skull, coupled with the frequency of evolutionary convergence in the morphology of the feeding apparatus (e.g. Langston 1973) leave systematists with few alternative character states upon which to build systematic hypotheses. Within the limitations of the data used here, the expression of character states 1 to 11 in *Harpacochampsa camfieldensis* suggests that this taxon belongs with crocodylids (Table 2, Fig. 9). Because the palatal region is not known, no firm conclusion can be drawn about its systematic position within crocodylids.

Character states 12 to 18 (Table 2) and other comparisons made in the description serve to demonstrate that *H. camfieldensis* is phenetically dissimilar to its broad-snouted Australian contemporaries, convergent on *Gavialis gangeticus* in some respects, and in terms of sutural relationships, indistinguishable from extant *Crocodylus* species.

General Remarks. Densmore (1983) published results of the molecular systematics of extant species of the Order Crocodilia. corroborating many of the interpretations favoured by comparative morphologists, but departing from prevailing views by closely aligning the 'true' gavial, *Gavialis gangeticus*. with the 'false' gavial, *Tomistoma schlegelii*. Comparative morphologists (Romer 1956; Kälin 1955; Wermuth 1953) had previously interpreted the systematic position of *Tomistoma* in differing ways, but were united in their views that it was not closely related to *Gavialis*, and that any similarity was due to convergence.

Buffetaut (1985) reconciled morphological and molecular evidence for relationships within the Eusuchia by deriving gavialids from a tomistomid structural stage, and also pointed out that Densmore's (1983) hypothesis of relationship amongst living taxa is broadly concordant with stratigraphic evidence. Norell (1989) disagrees with this systematic interpretation, presenting a cladistic analysis of 12 morphological character states that supports Dumeril's (1806) hypothesis that gavialids are the sister group of all other Eusuchians, and

CHARACTER		*Gavialis gangeticus*	ALLIGATORIDS	*Baru*	*Pallimnarchus*	*Australosuchus*	*Quinkana*	*Brachyuranochampsa*	*Tomistoma schlegelii*	*Osteolaemus*	*Crocodylus porosus*	*C. acutus*	*C. johnstoni*	*C. cataphractus*	*Harpacochampsa camfieldensis*
1.	posterior, intrapterygoid position of internal nares	+	+	+	+	+	?	+	+	+	+	+	+	+	+
2.	loss of postorbital spine	-	+	+	+	+	?	+	-	+	+	+	+	+	+
3.	reduced pro-otic exposure	-	+	?	?	?	?	?	-	+	+	+	+	+	+
4.	reduced basisphenoid exposure	-	+	?	?	?	?	?	-	+	+	+	+	+	+
5.	loss of posterior ectopterygoid process along jugal	-	-	+	+	+	?	?	+	+	+	+	+	+	+
6.	quadratojugal-jugal suture enters posterior angle of infratemporal fenestra	-	-	+	+	+	?	?	+	+	+	+	+	+	+
7.	fourth dentary tooth enters rostral pit	-	+	-	-	-	-	-	-	-	-	-	-	-	-
8.	enlarged fourth maxillary tooth	-	+	-	-	-	-	-	-	-	-	-	-	-	-
9.	loss of quadratojugal spine	-	+	-	-	-	?	+	-	-	-	-	-	-	-
10.	loss of anterior palatine process	-	-	+	+	+	+	+	?	-	-	-	-	-	?
11	interlocking dentition	+	-	-	-	-	-	-	+	+	+	+	+	+	+
12.	nasals enter narial aperture (sometimes below premaxillary overgrowth)	-	+	-	+	+	+	+	-	+	+	+	+	?.	+
13.	proportional degree of elongation of premaxilla on palatal surface (1 = short, 3 = long)	2	1	1	1	?	1	1	3	1	1	1	2	2	1
14.	supratemporal fenestra "open"	+	-	-	-	?	?	-	-	-	-	-	-	-	+
15.	slit-like expression of foramen for orbito-temporal artery	+	-	-	?	?	?	?	-	-	-	-	-	-	+
16.	premaxillary teeth largest in rostral series, premaxilla proportionally expanded	+	-	-	-	?	-	-	-	-	-	·	-	-	+
17.	relative size of supratemporal fenestra (1=small, very large=3)	3	1	1	1	?	?	2	2	1	1	1	2	2	3
18.	robustness of jugal bounding infratemporal fenestra	1	3	3	3	?	?	3	3	3	3	3	3	3	1

Table 2. Selected character states represented on the *Harpacochampsa camfieldensis* holotype compared with the condition in other Eusuchian taxa. Polarity of character states are discussed in the text. '+' denotes presence of a feature, '-' denotes absence. Character states 1 to 11 are considered to have systematic value, and their description has been phrased so that their presence may be regarded as the derived condition. Character states 12 to 18 are considered to be functionally related and are not reliable systematic indicators on the basis of current understanding.
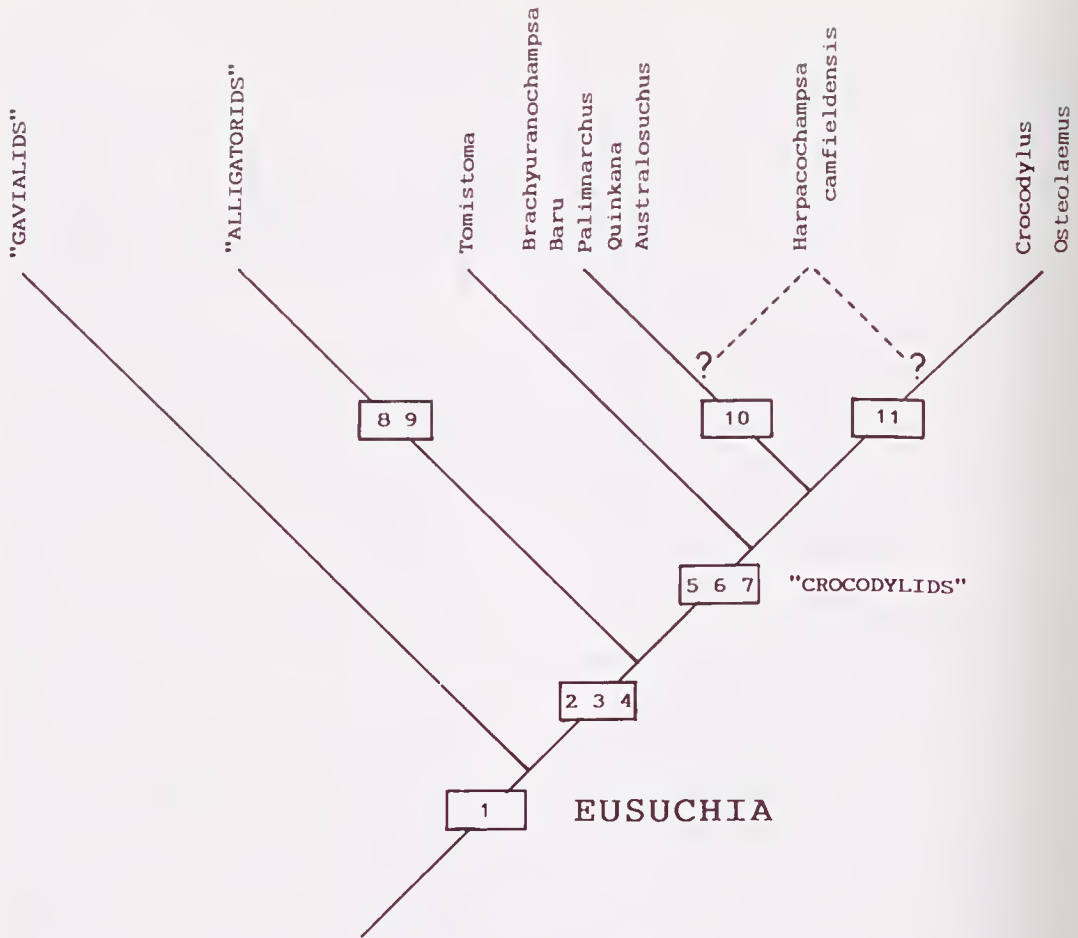
Fig. 9. A hypothesis of relationship of selected Eusuchian taxa using character states listed in Table 2. This suite of character states resolves *H. camfieldensis* as a crocodylid, but cannot resolve its position within the group.

that tomistids belong with crocodylids as the sister group to alligatorids.

Tarsitano *et al.* (1989) and Frey *et al.* (1989) describe additional features distinguishing *G. gangeticus* from all other extant Eusuchians, but the systematic significance of these character states is not clear and, on the basis of current understanding, do not necessarily preclude the evolution of gavialids from a tomistomid structural stage. Nonetheless, these workers interpret *G. gangeticus* as an Eusuchian relict, remote from other Eusuchians.

Fossil gavialids are sometimes difficult to distinguish from fossil tomistomids. Hecht and Malone (1972) list character states by which these forms can be distinguished. The question of gavialid, tomistomid and crocodylid relationship is of interest here because *H. camfieldensis* retains some features consid-

ered diagnostic of gavialids. These include the morphology of the supratemporal fenestra and associated structures, specifically: the size of the supratemporal fenestra and its lack of partial 'closure' by expansion of the squamosal and parietal below the level of the skull deck; slit-like expression of the foramen for the tempero-orbital artery within the posterior wall of the supratemporal fenestra; and broad squamosal overlap of the quadrate in dorsal view (proportionally large skull table). Although the Camfield crocodile does not quite reach the extremes of expression for some of these characters as seen in *G. gangeticus*, these features are fully developed, correspond quite closely to some fossil gavialids, and cannot be interpreted as structural intermediates to other Eusuchians. Additionally, the new taxon parallels *G. gangeticus* in the proportional en-

largement of the premaxillary teeth, a gracile, straight jugal, and robust postorbital bar. Unlike *Gavialis*, the cranial bones are arranged as in *Crocodylus*, the skull is fully 'verticalised' *sensu* Tarsitano *et al.* (1989), basioccipital tuberosities are absent, the postorbital bar lacks a spine, nasals enter the external nares, the orbits are almost certainly not everted, and the rostrum probably tapers smoothly, as shown in Figure 2, in the typical crocodylid fashion. It seems most likely that the morphology of the skull table, jugal, and supratemporal fenestra are part of a functional complex, perhaps associated with a proportionally enlarged premaxillary dentition. Apart from these features, the Camfield crocodile shares few others with *Gavialis*.

Functional aspects of the skeleto-muscular system of crocodilians are described from a general perspective by Schumacher (1973) and Iordansky (1964, 1973), while Busbey (1989) presents a more detailed analysis of cranial-muscle function in *Alligator mississippiensis.* Iordansky (1964, 1973) offered explanations of the relationship of the degree of development of cranial structures to trophic adaptation and muscle function in various extant Eusuchians; more recent refinements are reviewed in Busbey (1989).

In the following review, we consider the mechanics of the skeleto-muscular system from the point of view of evolution towards extreme longirostry or towards brevirostry, using Schumacher (1973: figs 32 - 34) as a starting point. The model outlined here is necessarily simplistic. A recent discussion of factors influencing skeleto-muscular function, and approaches to functional interpretations, may be found in Gans and de Vree (1987), and Gans (1988).

As the skull becomes elongated, the jaws need only be rotated through a few degrees to achieve an effective gape at the level of the premaxillae. As a consequence, the pterygoid flange need only be short in order to serve its function in guiding the jaws during closure and opposing the medial traction component of the adductor complex (Schumacher 1973). The pterygoid muscle complex becomes increasingly ineffective because its line of action comes closer to paralleling the jaws, especially as they approach complete closure. The M. adductor mandibularis externus profundus (= M. pseudotemporalis of Iordansky 1973:

Busbey 1989), inserting dorsally largely within the supratemporal fossa and ventrally on the mandibular adductor tendon lamina intramandibularis (intramandibular tendon of Schumacher 1973), retains a very favourable perpendicular line of action to the jaws, and thus within the constraints of crocodilian skeleto-muscular architecture, is likely to be selected for at the critical point at which the pterygoid complex can no longer effectively adduct the jaws. This point probably depends on three factors: the length of the load arm (i.e. the jaw), its mass, and potential within the skull architecture for development of the various muscle groups. Correspondingly, the diductor complex must be enlarged to open the jaws: on land, with the lower jaw resting on the ground surface, crocodilians open their jaws by raising the upper jaw. This posture precludes opening the jaws simply by relaxing the adductor complex and allowing the lower jaw to sag under gravity, in the manner of most tetrapods, while in the water viscous drag also requires active diduction of the jaws. In *Gavialis*, these features can be correlated with small palatal fenestrae, large 'open' supratemporal fenestrae, and long retroarticular processes on the jaws. The degree of longirostry of the Camfield crocodile can only be inferred, but on the basis of its structural correspondence with *G. gangeticus*, it may have reached a similar functional turning point at which enlarged adductor mandibularis externus profundus muscles become advantageous.

In contrast, brevirostrine crocodilians must rotate the jaws through a considerably greater arc to achieve an effective gape, need a much longer pterygoid flange, and the line of action of the pterygoid muscle complex remains effective throughout the range of closure. The M. adductor mandibularis externus profundus contribute little to the power of the jaws.

The general inverse correlation in the size of the supratemporal and palatal fenestrae, and the corresponding size of the muscle masses occupied by them, was noted long ago (eg Gadow 1901). The proportionally largest supratemporal fenestrae are found in the extremely long-snouted, extinct teleosaurs and metriorhynchids. Busbey (1989) suggests that in these forms the M. adductor mandibularis externus profundus contributed as much as 50% of the adductor muscle mass. At the other extreme, the supratemporal fenestrae may be

closed over, as in some individuals of the brevirostrine genera *Osteolaemus* and *Paleosuchus*. Busbey (1989:122) suggests that in the crocodilian skull. only the M. adductor mandibularis externus profundus and anterior pterygoid muscle are in physical positions amenable to enlargement or reduction in size, and that their relative contribution to the adductor complex is selected for to maintain optimum adductor moment throughout the range of jaw-gape.

Within this model there is great scope for variation in the expression of muscle development and skeletal correlates, depending on skull conformation (e.g. length, depth, breadth) and the degree of robustness or gracility, but the range of possibilities for crocodilians is finite, and functional convergences are common (Langston 1973). As outlined above, the degree of longirostry alone need not dictate the relative development of cranial structures and associated muscles. Thus, some of the differences between tomistomids and gavialids (Hecht and Malone 1972) may be functionally-related and may not preclude close relationship.

Tarsitano *et al.* (1989) point out that cranial 'verticalisation' in crocodilians is related to the development of the pterygoid flange, and observe that the 'unverticalised' condition of *Gavialis* resembles the condition in post-hatchling *Alligator*. Because Mesozoic Mesosuchian teleosaurs, most other Mesozoic reptile groups. and at least some post-hatchling extant crocodilians also have an unverticalised cranium. these workers have interpreted the condition to be primitive in the gavial, and implied that verticalisation is a synapomorphy of all other Eusuchians. Because convergences within crocodilians are common, and diagnostic features of taxa are often trophically dedicated, it seems useful to consider function before interpreting the systematic significance of the expression of a particular character state. Because a gavial can operate effectively with a short pterygoid flange, a suitable pre-adaptation may have been selected for in favour of a structural reversal, and evolve independently in Mesosuchian and Eusuchian lineages. Similarly, basioccipital tuberosities are almost certainly functionally-related (eg Langston 1973) and their presence may be associated with the derived selection of a paedomorphic, unverticalised neurocranium. The possibility that the gavial is paedomorphic

has been considered by Iordansky (1973). Buffetaut (1985) and Norell (1989), and this factor is critical to the correct interpretation of the polarity of the character complex associated with neurocranial verticalisation. Functional considerations lead us to the conclusion that *H. camfieldensis* is convergent on *Gavialis*, and also suggest that gavialids, though highly distinctive. may not be so remote systematically from tomistomids and crocodylids.

Tarsitano *et al.* (1989:843) suggest that *Tomistoma* is 'merely another member of the genus *Crocodylus* within the Eusuchia'. We agree that *Tomistoma* may be a crocodylid, but such a taxonomic revision seems premature. Our interpretation of extinct Australian genera suggests that crocodylids may be paraphyletic (but not polyphyletic), and Zangerl's (1944) inference that *Brachyuranochampsa* may be close to *Tomistoma* warrants further examination.

Palaeozoogeography and Palaeobiology. The broad-snouted extinct Australian genera are possibly members of a natural group of relatively archaic crocodylids that retain an overbite dentition, perhaps closely related to the Eocene *Bachyuranochampsa eversolei* from North America (Willis *et al.* 1990). The fossil evidence suggests that an Australian radiation persisted in the form of *Quinkana* and perhaps *Pallimnarchus* into the Australian Pleistocene (Molnar 1981, 1982a), long after similar crocodilians evidently became extinct in North America. In Willis *et al.* (1990) we suggest that their persistence in Australia resulted from geographic isolation following the final break-up of Gondwana. All these taxa have been recovered from freshwater sediments, and their capacity for marine dispersal is not known.

The extant estuarine crocodile, *Crocodylus porosus*, is the earliest Australian representative of *Crocodylus*, and first appears in Pliocene sediments (Molnar 1979). Palaeontological and molecular evidence indicates a relatively recent geological history for *Crocodylus* (e.g. Densmore 1983), though the genus has been used by palaeontologists as a 'waste basket' into which many problematic and poorly represented forms have been placed (Taplin and Grigg 1989) extending back into the Mesozoic. The capacity of *Crocodylus* for a geologically-recent circumtropical marine dispersal is probably related to an ability to maintain osmotic balance in the marine realm by

excreting salt from sub-lingual glands (Taplin and Grigg 1989). *Crocodylus* probably entered Australia from the north as the Australian crustal plate approached Asia during the Neogene (Audley-Charles 1981).

At present, the only basis for the hypothesis that *Brachyuranochampsa* and some Australian fossil genera comprise a natural group of crocodylids is the morphology of the anterior palatine process. This critical portion of the anatomy of *Harpacochampsa camfieldensis* is not yet known, and it is possible that *H. camfieldensis* is a member of this Australian radiation, though a phenetic comparison of the available material does not compel one to such a conclusion. On the other hand, positive evidence available in the form of close structural concordance with *Crocodylus*, and the lack of discrete features aligning *H. camfieldensis* closely with other Eusuchians, raises the possibility that the new taxon is a congener of *Crocodylus*. In this scenario, *H. camfieldensis* is envisaged as originating in Asia, crossing relatively short stretches of open ocean and insinuating itself as a specialist piscivore. It would thus become the earliest representative of '*Crocodylus*' in Australia.

A cranial table, anterior dentary fragment and premaxilla from the Alcoota Local Fauna (late Miocene or early Pliocene) of central Australia was referred to *Crocodylus* by Woodburne (1967:Plate 7). The Alcoota crocodile (assuming the fragments represent a single taxon) appears to be a pseudoheterodont, broad-snouted form, with small supratemporal fenestrae, short dentary symphysis, small first dentary tooth, and closely spaced premaxillary teeth which closed outside the dentary teeth in an 'overbite' configuration. In general, it resembles extinct Australian broad-snouted forms and probably does not belong with *Crocodylus*.

Observations of living crocodiles of different species with an overlapping range indicate that juvenile and sub-adult crocodiles are often in direct competition, feeding on a wide range of animals, including invertebrates, amphibians and small reptiles, birds and mammals. Individuals of a species may not occupy the specialised ecological niche for which they are adapted until they reach maturity. Morphological, taphonomic and sedimentological evidence suggest that *H. camfieldensis* and the other crocodile of the Bullock Creek Local Fauna, *Baru darrowi*, played complimentary ecological roles as adults.

Based on the skull dimensions of the holotype, and by comparison with living crocodiles, *H. camfieldensis* probably grew up to a length of four metres. The holotype was recovered from a massive calcilutite which contains an abundance of fish remains, including lungfish. This lithology rarely contains rich concentrations of fossils such as those found nearby in coarse, stream-channel deposits where terrestrial elements of the Bullock Creek Local Fauna are concentrated. The teleost fish so far recovered are small, but the lungfish probably grew to a length of up to 80 cm (A. Kemp, pers. comm.). Chelid turtles are also present. The texture of the sediment suggests a relatively quiet depositional environment; perhaps a billabong of a river system. Thus *H. camfieldensis* may have occupied deeper, sluggish pools, feeding principally on fish and possibly turtles; its somewhat stout build and powerful anterior dentition suggests it was capable of dealing with other prey up to medium-sized mammals, but perhaps unlike *Baru*, it may have had to drag such prey into deeper water to weaken it by drowning and deny it purchase in its struggles.

In contrast, *Baru darrowi* is a very powerful, broad-snouted crocodylid which grew to a length of five metres or more. It is common in the coarser stream-channel deposits. *Baru* may have ambushed its prey, including large mammals, near the banks of shallow streams and dispatched them by shock-induced trauma from its powerful bite (Willis *et al.* 1990).

CONCLUSIONS

1. *Harpacochampsa camfieldensis* is functionally convergent on *Gavialis gangeticus*, but close systematic relationship is not indicated.

2. The new taxon retains morphological features considered by Hecht and Malone (1972) to be diagnostic of gavialids, but unlike *Gavialis gangeticus*, the neurocranium of *H. camfieldensis* is fully 'verticalised' *sensu* Tarsitano *et al.* (1989). Functional considerations suggest some of these features are trophically dedicated and perhaps not clear indicators of phylogeny. Juvenile Eusuchian features, representing advantageous pre-adaptations for longirostry, may have been selected for in the gavial, and it is

possible that the gavial, though highly distinctive, may not be systematically remote from crocodylids and tomistomids.

3. The character states by which *H. camfieldensis* may be compared with extant Eusuchians and extinct Australian genera (Table 2) cannot adequately resolve Eusuchian relationships at higher taxonomic levels, but are sufficient to demonstrate that the new fossil is a crocodylid.

4. The palatal region of the *H. camfieldensis* is not known, and the question of whether it is systematically linked with extinct broad-snouted Australian crocodylids, or is more closely related to *Crocodylus,* cannot yet be answered.

ACKNOWLEDGEMENTS

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